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NEST SITE USE BY CAVITY-NESTING BIRDS OF THE CARIBOO PARKLAND, BRITISH COLUMBIA

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Several birds and mammals build their nests in cavities located in the trunks or large branches of dead or dying trees. Many of these species are secondary cavity nesters and use natural cavities formed by decay or, more commonly, excavated by primary cavity nesters such as woodpeckers (Zeleny 1977). Cavity-nesting is advantageous because cavities protect the brooding female and the offspring from weather and predators (von Haartman 1957, Zeleny 1977). Consequently, breeding success of cavity nesters is generally much higher than that of other birds.

One drawback of cavity nesting is that inter- and intraspecific competition for nest sites may be severe. Several lines of evidence show that natural cavities are often limited: (1) addition of nest boxes has resulted in large increases in populations of some hole nesters (von Haartman 1957, Strange et al. 1971, Hamerstrom et al. 1973); (2) all suitable cavities are sometimes used by cavity nesters (van Balen et al. 1982); and (3) interspecific competition has been observed in the form of fights between nesting birds or destruction of nests by competitors (von Haartman 1957; Erskine 1959, 1964, pers. obs.).

The availability of suitable nest sites may therefore be critical in determining population numbers and community composition among secondary cavity nesters. Snyder (1977) proposed three levels of limitation for these cavity nesters. First, there may be an intrinsic scarcity of adequate nest sites relative to other necessary resources. Second, the suitability of a nest site might be constrained by its vulnerability to competitors and predators. Third, there may be behavioral limitations in the abilities of species to locate existing nest sites.

The interior of British Columbia has a rich cavity-nesting community (McLaren 1963). In the early fifties, the European Starling (*Sturnus vulgaris*) invaded the area, and Erskine and McLaren (1976) predicted that competition for nest sites would increase as a result of this change in the avian community. The objectives of this study were to (1) characterize differences in nest sites among six cavity-nesting species, (2) compare nest site characteristics found in this study with similar data collected by McLaren (1963) 24 years ago, and (3) assess the degree of competition for nest sites in this community in relation to presence of starlings.

METHODS

The study was conducted 15 km north of 100 Mile House in the Cariboo Parkland region of British Columbia. The study area covers about 20 km^2 of rolling grassland, small groves of aspen (*Populus tremuloides*), and boreal forest of Douglas fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*). Although boreal forest is dominant in the general area, about ⅔ of the study area was located in the parkland habitat. The study area included eighteen ponds and two lakes ranging in size from <1 ha to 60 ha.

Cavities were located by intensive searches of all suitable trees. Most of the searching effort was concentrated on trees within 200 m of the ponds and lakes from the first week of May to the beginning of July 1983. Overall, about 250 ha were searched thoroughly for cavities. Each cavity was mapped, marked with flagging tape, and revisited at least twice to determine if the cavity was being used, and by what species. Cavities were reached using ladders or spurs, and they were inspected with a periscope (De Weese et al. 1975). A cavity was labeled as empty if no eggs or fresh nesting material had been detected by the end of July.

McLaren (1963) divided the hole-nesting community of the Cariboo in three cycles according to the size of the cavity and its primary cavity nester: the small cavity cycle of the Yellow-bellied Sapsucker (*Sphyrapicus varius*), the midsize one of the Northern Flicker (*Colaptes auratus*), and the large one of the Pileated Woodpecker (*Dryocopus pileatus*). Our study concentrated on cavities of the "flicker cycle," which are the most abundant in the area. Species using flicker cavities form a discrete community except for the Tree Swallow (*Tachycineta bicolor*), which readily uses both sapsucker and flicker cavities (McLaren 1963). Thus, species included in this study used only flicker cavities (>4.5 cm in entrance diameter), except for the swallows, which used cavities >3.5 cm in entrance diameter.

All nest sites where the resident species was known were measured, except for cavities occupied by starlings and swallows, where we randomly selected 43 and 31 cavities, respectively, for measurement. A few cavities were used by two species at different times during the breeding season. In such cases, we included that cavity's measurements twice (once for each species) in the analysis. Measurements were made near the end of July after young had fledged from the nests.

Nineteen variables were measured at each nest site. Habitat variables included: the dominant tree species, an index of tree density in the grove, and the height of the understory vegetation. The basal area was used as an index of tree density. Basal area was measured one m in front of the tree using a forester prism (basal area factor of 6 m^2/ha/tree).

The six variables describing the nesting tree included: the diameter at breast height, the height of the nesting tree, the canopy height from the ground to the bottom of the crown canopy, the distance to water (pond or lake), the distance to the nearest obstruction in front of the cavity entrance, and the distance to the nearest edge of the stand of trees. Canopy height was measured using a surveyor level, and snags in open areas were assigned a value of 20 m, the highest canopy measured in this study. We also noted the tree species and whether the tree was dead or alive.

Ten cavity variables included: the horizontal and vertical diameter of the entrance, the compass direction that it faced, the height of the entrance above the ground, the depth of the cavity from the bottom edge of the entrance to the floor, the breadth from the inside edge of the entance to the back wall, and the width between the two side walls at the entrance level. Width and breadth were measured using a collapsing ruler; depth was measured using a plumb bob. We used these inner dimensions to calculate the volume of the cavity (depth × breadth × width), the floor area ($\pi \times \frac{1}{2}$ breadth $\times \frac{1}{2}$ width), and the area of the cavity entrance ($\pi \times \frac{1}{2}$ vertical $\times \frac{1}{2}$ horizontal diameter). In addition, we noted the type of nesting material, if any, within the cavity.

A few variables were not normally distributed, and these were transformed by log(x + 1) to allow the use of parametric statistics (Sokal and Rohlf 1969:384). We first performed a one-way analysis of variance (ANOVA) on each variable to test for differences among species.

A discriminant function analysis (DFA) was then performed to characterize the type of cavity used by each species. Only variables that were statistically significant (using the criterion $P < 0.1$) in the ANOVA were included in the DFA. This procedure reduces the number of variables in the DFA and eliminates variables that contribute little a priori to separation among groups (Pimentel 1979, Mackenzie and Sealy 1981). Correlations among cavity measurements were checked to ensure that they were not highly dependent.

The DFA uses the observed variables to produce a linear function that maximizes separation among species by maximizing among-group to within-group sums of squares (Jeffers 1978, Williams 1983). The accuracy of the discriminant function model was evaluated using the Jackknife procedure (Jeffers 1978, Williams 1983, Willner et al. 1983). This method makes efficient use of cases, as one case is omitted each time a discriminant function is computed. This model is then used to classify independently the excluded cases. Statistical analyses were performed with the MDA computer program.

RESULTS

Of the 311 cavities found, 176 (57%) were occupied at some time during the breeding season. Nine different species used these cavities: starling (44%), Tree Swallow (19%), Bufflehead (*Bucephala albeola*) (15%), Northern Flicker (8%), Mountain Bluebird (*Sialia currucoides*) (4%), flying squirrel (*Glaucomys sabrinus*) (3%), American Kestrel (*Falco sparverius*) (2%), Northern Saw-whet Owl (*Aegolius acadicus*) (2%), and red squirrel (*Tamiasciurus hudsonicus*) (2%). Kestrels, owls, and red squirrels were deleted from the following analysis because of small sample sizes ($N < 5$).

Unlike cavity excavators, most secondary cavity nesters line their nest with vegetation or feathers (pers. obs.). Among the 135 unoccupied cavities, only 6 contained no nesting material and therefore showed no sign of previous use by any secondary cavity nesters. We did not determine, however, the proportion of unused cavities that were still suitable. Eighty-three percent of the used cavities were in aspens and 47% were in dead trees.

Univariate analysis.—Eighteen variables were tested using ANOVA to see if they varied significantly among the 6 species (dominant tree species was excluded since it is a discrete variable). The results (Table 1) showed that the following 6 variables were not significant ($P > 0.1$): tree density, height of understory, height of nesting tree, distance to water, compass direction of the entrance, and height of the entrance. These variables were eliminated. The cavity variables differed much more among species than did the habitat or nest tree variables (Table 1). Entrance diameter and inner cavity dimensions were also deleted from the remaining analysis as these variables were highly correlated with entrance area and cavity volume.

TABLE 1

RESULTS OF ONE-WAY ANALYSIS OF VARIANCE FOR 18 VARIABLES CHARACTERIZING NEST SITES OF 6 SPECIES OF CAVITY NESTERS IN THE CARIBOO PARKLAND, BRITISH COLUMBIA[a]

Variables	F values	P
Habitat variables		
Tree density	1.808	0.12
Height of understory	1.572	0.14
Tree variables		
DBH of nesting tree	2.282	0.051
Height of nesting tree	0.438	0.90
Canopy height	5.746	<0.001
Nearest water	1.210	0.31
Nearest entrance obstruction	1.914	0.097
Nearest edge of stand	2.278	0.052
Cavity variables		
Compass direction	1.082	0.37
Height of cavity entrance	0.631	0.67
Cavity volume	25.402	<0.001
Entrance area	5.937	<0.001
Floor area	15.511	<0.001
Vertical entrance diameter	2.869	0.018
Horizontal entrance diameter	4.694	<0.001
Width of cavity	15.594	<0.001
Breadth of cavity	8.495	<0.001
Depth of cavity	8.300	<0.001

[a] See Table 2 for sample sizes.

Swallows and bluebirds were found to occupy the smallest cavities, flickers and Buffleheads occupied the largest ones, and starlings and squirrels occupied intermediate sized cavities (Table 2). Nest sites of flickers, Buffleheads, and bluebirds were characterized by having few obstructions in front of the cavity entrance. Bluebirds tended to nest in open habitat, flickers and Buffleheads in sparsely treed groves, starlings on the edges of dense stands, and squirrels within denser forests (Table 2).

Multivariate analysis.—Species with small sample size ($N < 14$) were excluded from the DFA, as suggested by Williams (1983). The analysis thus included only starlings, swallows, Buffleheads, and flickers. The test for homoscedasticity showed that the variance-covariance matrices were homogeneous (Box's $M = 85.2$, $F = 1.187$, df $= 63,9743$, $P > 0.1$).

Three discriminant functions were derived from the analysis, although only the first two were significant (χ^2 test, $P < 0.05$) (Table 3). These two factors accounted for 97.2% of the discriminating power of the model.

TABLE 2

CHARACTERISTICS OF NEST SITES FOR 6 CAVITY-NESTING SPECIES OF THE CARIBOO PARKLAND, BRITISH COLUMBIA

	Bufflehead	Northern Flicker	European Starling	Mountain Bluebird	Tree Swallow	Flying squirrel
N	26	14	41	7	31	6
Tree density (m^{2}BA[a]/ha)	27 ± 3[b]	21 ± 4	35 ± 4	22 ± 9	33 ± 4	40 ± 7
DBH (cm)	33.0 ± 1.4	30.0 ± 2.0	31.1 ± 1.1	29.1 ± 1.8	27.3 ± 0.9	30.4 ± 2.9
Canopy height (m)	9.1 ± 1.5	16.5 ± 1.6	5.9 ± 0.7	6.4 ± 2.4	9.1 ± 1.2	9.0 ± 2.4
Nearest entrance obstruction (m)	7.7 ± 0.7	9.1 ± 0.6	7.1 ± 0.6	10.0 ± 0.1	6.6 ± 0.7	5.9 ± 1.9
Nearest edge of stand (m)	5.0 ± 1.1	5.1 ± 1.6	2.2 ± 0.5	0.4 ± 0.4	3.5 ± 1.1	4.7 ± 2.1
Vertical entrance diameter (cm)	7.4 ± 0.5	7.5 ± 0.3	6.9 ± 0.4	7.0 ± 1.1	5.5 ± 0.4	5.9 ± 0.4
Horizontal entrance diameter (cm)	6.8 ± 0.1	6.9 ± 0.5	6.3 ± 0.2	5.8 ± 0.7	5.2 ± 0.3	6.1 ± 0.3
Width of cavity (cm)	14.0 ± 0.4	13.3 ± 0.6	12.4 ± 0.4	9.7 ± 1.3	8.9 ± 0.4	11.8 ± 0.5
Breadth of cavity (cm)	15.7 ± 0.6	14.9 ± 0.6	15.0 ± 0.5	12.7 ± 0.9	11.6 ± 0.4	13.0 ± 1.1
Depth of cavity (cm)	35.3 ± 3.0	33.7 ± 2.5	26.4 ± 1.7	19.9 ± 5.1	17.5 ± 1.7	26.7 ± 2.1
Volume of cavity (cm^3)	6212 ± 698	5251 ± 537	3831 ± 303	2362 ± 990	1534 ± 249	3149 ± 229
Floor area (cm^2)	175 ± 10	158 ± 12	149 ± 8	97 ± 15	82 ± 5	123 ± 15
Entrance area (cm^2)	40.4 ± 3.3	40.5 ± 3.0	34.6 ± 3.2	35.3 ± 10.8	23.8 ± 2.1	28.1 ± 2.4

[a] BA: basal area.

[b] Mean ± SE.

TABLE 3

SUMMARY OF DISCRIMINANT FUNCTION ANALYSIS PERFORMED ON NEST SITE CHARACTERISTICS OF STARLINGS, SWALLOWS, BUFFLEHEADS, AND FLICKERS

Variables	Correlation between canonical vectors and variables		
	I	II	III
DBH	−0.270	0.214	−0.234
Canopy height	0.011	−0.889	−0.053
Nearest entrance obstruction	−0.142	−0.261	0.168
Nearest edge of stand	−0.077	−0.233	−0.875
Cavity volume	−0.987	−0.010	0.112
Entrance area	−0.490	−0.242	0.097
Eigenvalue	1.159	0.273	0.042
Percentage of variance explained	78.6	18.6	2.8
Canonical correlation	0.733	0.463	0.200

Correlations between the canonical vectors and the original variables were used to assess the importance of the original variables on each canonical axis as suggested by Williams (1983). The first axis was dominated by cavity volume, and to a lesser extent by entrance area. The second axis was strongly influenced by canopy height. Finally, the third axis was characterized by the distance to nearest edge of the stand (Table 3).

The DFA, however, resulted in only 62% of correct classification. Classification of starling and swallow cavities was relatively good (Table 4), however, Bufflehead cavities were classified as starling cavities almost as often as they were classified as Bufflehead cavities, and many flicker cavities were classified as starling cavities. The 95% confidence circles in Fig. 1 show that, according to our model, there was nearly total overlap

TABLE 4

CLASSIFICATION MATRIX OF NEST SITE CHARACTERISTICS USING STARLINGS, SWALLOWS, BUFFLEHEADS, AND FLICKERS BASED ON THE JACKKNIFE PROCEDURE[a]

Actual group	N	Predicted group (%)			
		Starling	Swallow	Bufflehead	Flicker
Starling	43	65	16	19	0
Swallow	31	13	77	3	6
Bufflehead	26	35	0	46	19
Flicker	14	14	0	36	50

[a] Overall percentage of groups correctly classified is 62%.

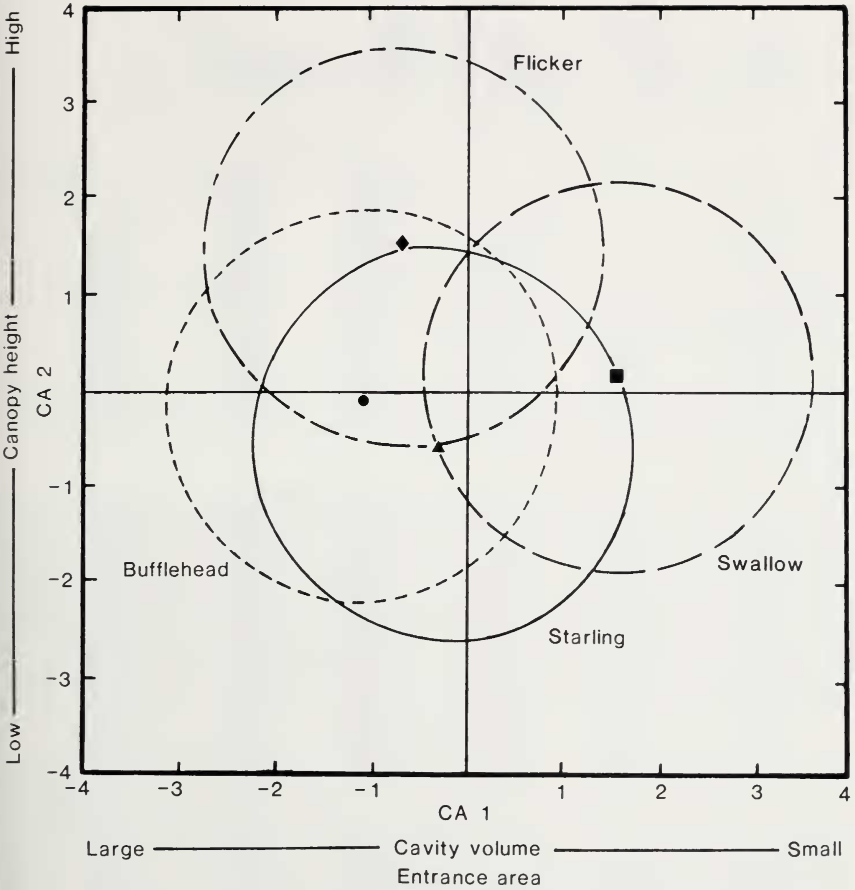

FIG. 1. Plot of centroids and 95% confidence circles of nest site characteristics for 4 species of cavity nesters on the first and second canonical axes.

between Buffleheads and starlings in cavity use. Flickers also overlapped with Buffleheads and starlings, whereas swallows overlapped less with flickers and Buffleheads.

As starlings have recently invaded this community, and as they showed the greatest overlap with other species in cavity use, we performed the DFA again using only swallows, Buffleheads, and flickers. The discriminant functions obtained were identical to those of the previous analysis; however, the accuracy of the classification improved to 82% (Table 5).

Comparison with previous data.—McLaren (1963) conducted a similar study in the same area 24 years ago, when starlings had just invaded the community. Although he had large sample sizes, his measurements were restricted to the cavity itself, thus limiting the extent of a comparison

TABLE 5

CLASSIFICATION MATRIX OF NEST SITE CHARACTERISTICS USING ONLY SWALLOWS, BUFFLEHEADS, AND FLICKERS BASED ON THE JACKKNIFE PROCEDURE[a]

Actual group	Predicted group (%)			
	N	Swallow	Bufflehead	Flicker
Swallow	31	90	3	6
Bufflehead	26	4	85	12
Flicker	14	14	29	57

[a] Overall percentage of groups correctly classified is 82%.

between the two studies. As McLaren's data included only flicker holes, we excluded individuals (mostly swallows) using sapsucker cavities from our data.

Cavity depths measured in this study differed from McLaren's data only for bluebirds, which used significantly deeper cavities (Fig. 2). The breadth of all flicker cavities was significantly smaller than in McLaren's data; however, there was no difference for any species taken separately, except for swallows, which had significantly narrower cavities. Finally, the entrance areas of our cavities were significantly smaller than in McLaren's data for all species but bluebirds, where the trend was similar.

DISCUSSION

Nest site characteristics.—Our data show that volume of the cavity and, to a lesser extent its entrance area, were the most important variables in determining species occupancy. Entrance size certainly limits cavity use by a particular species as there is a minimum size of hole that an individual can pass through. In addition, individuals may select the smallest hole possible to avoid eviction by a larger species or predation (Moed and Dawson 1979). It is surprising, however, that the volume of the cavity is more important than is entrance size in determining species occupancy. Zeleny (1977) and Moed and Dawson (1979) found that reproductive success in several species of birds was related to the inner cavity dimensions. They also found that cavity floor area affected clutch size, and that the depth of the cavity below the entrance was inversely related to losses owing to predation.

Why should height of the canopy, the dominant variable on the second canonical axis, be an important factor in determining cavity use? It is possible that canopy height influences access to the cavity, so that birds with low maneuverability prefer trees with a high canopy. Fig. 1, however, shows that flickers, which are the sole excavators of cavities in this group

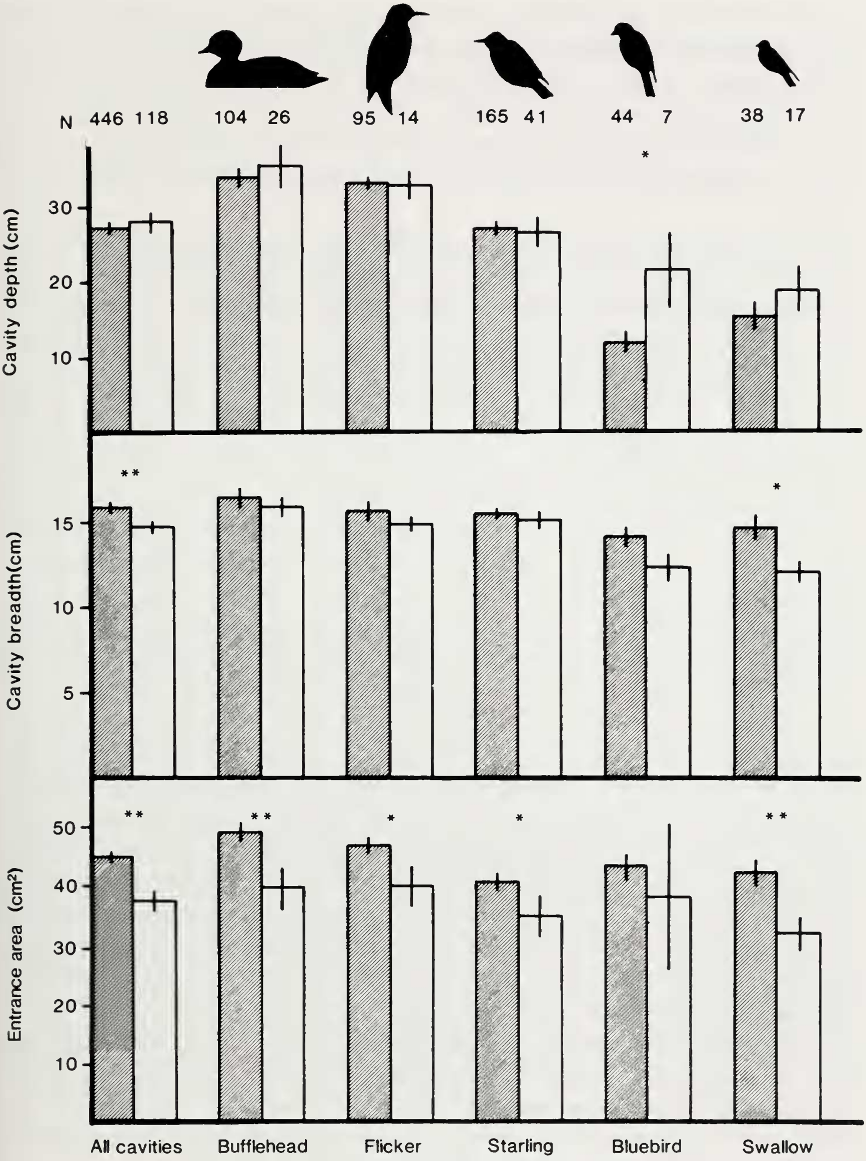

FIG. 2. Comparison of cavity dimensions found in this study (open bars) with similar data collected 24 years ago (calculated from McLaren 1963) (hatched) for 5 species of cavity nesting birds in the Cariboo parkland, British Columbia. Bird silhouettes are approximately scaled to relative body size. Mean ± SE (*t* test, * $P < 0.05$, ** $P < 0.01$, otherwise $P > 0.05$).

and thus should overlap the most with other species, are really the only species separated by canopy height. One explanation could be that cavities in high canopy trees are not available to secondary cavity nesters. We found that dead trees had a higher canopy than live ones (*t*-test, $P < 0.05$). The high canopy trees used by some flickers could have a shorter lifespan, falling earlier and thus becoming unavailable to secondary cavity nesters.

Interaction between starlings and other species.—The first record of starlings breeding in the Cariboo was in 1951 (Myres 1958). In 1959, McLaren (1963) found a large overlap in cavity use between starlings and other species. Erskine and McLaren (1976) later predicted that, because of competition with starlings, (1) flicker density would decrease, (2) cavities would become scarcer, and (3) competition for nest sites would intensify in this community. The percent of cavities occupied by starlings increased from 25% ($N > 450$, McLaren 1963) in 1959 to 44% ($N = 176$) in 1983. This suggests that starling populations have continued to increase and that competition for nest sites may have intensified. If competition has increased, we would expect a decrease in resource overlap among species (Mac Arthur 1972).

We looked at change in resource overlap by comparing our data with McLaren's data. The comparison suggests that some changes have indeed occurred in this community. The comparison is, however, limited in that data were collected by different observers in habitats that may have changed (e.g., through logging) in the past two decades. Fig. 2 shows that swallows and, to a lesser extent, bluebirds now use smaller cavities. Flicker cavities as a whole are also slightly smaller now, and these two species may merely be more opportunistic than others in their selection of nest sites. Alternatively, they may have been displaced from larger cavities by the more aggressive starling. This effect would be attenuated in swallows because they can use sapsucker cavities, a resource unavailable to other species. Bluebirds also use deeper cavities now, although the significance of this result is not clear to us.

Surprisingly, Buffleheads, which overlapped the most with starlings (Fig. 1), did not show any shift in cavity breadth or depth. We noted instances of Bufflehead nests being taken over by starlings (unpubl. data). Buffleheads, however, usually start nesting about 10 days before starlings and they may thus avoid being displaced by this species.

Cavities used in 1983 had a smaller entrance size than in 1959; however, all species were affected to the same extent, suggesting that the resource itself may have changed. Cavities excavated in Douglas fir last longer than those in aspens (Erskine 1978), and in fir trees the bark begins to rot before the tree falls, resulting in an enlarged cavity entrance (pers.

obs.). If McLaren's data included more fir cavities than ours (83% of our cavities were in aspen), this could account for the observed difference in entrance size. On the whole, cavity depth and breadth showed relatively little change compared to entrance size over the 24-year period between the two studies. This further strengthens the conclusion of the DFA that species have stricter requirements for inside cavity dimensions than for entrance size.

Despite the high overlap in cavity use, only 57% of the cavities found were used; however, the suitability of unused cavities was not assessed. Bluebirds and swallows tend to fill up cavities with nesting materials, making them unsuitable for species like Buffleheads and starlings (McLaren 1963). Unused cavities could have been older or more decayed as most aspens excavated for cavities have heartrot (Kilham 1971, Conner et al. 1976). Finally, some cavities may have remained unused because they fell within the territory of another individual. The distribution of cavities in our study was highly clumped (pers. obs.), and territorial species such as starlings, swallows, flickers, and bluebirds may have excluded conspecifics from suitable cavities.

It is not clear whether competition has intensified in this community despite the increase in starling abundance. Future research should quantify the availability of cavities in relation to their use by the different species.

SUMMARY

We studied nest site use by 6 species of cavity nesters in southcentral British Columbia. Discriminant function analysis was performed using nest site characteristics that differed significantly among 4 species (European Starlings, *Sturnus vulgaris*; Tree Swallows, *Tachycineta bicolor*; Northern Flickers, *Colaptes auratus*; and Buffleheads, *Bucephala albeola*). Cavity volume and, to a lesser extent, entrance area were the most important variables characterizing nest sites. Habitat variables were relatively unimportant except for canopy height, which also explained a significant amount of the variance. The analysis correctly classified only 62% of the cases, reflecting the high overlap in cavity use, especially between Buffleheads and starlings. We tested the prediction of Erskine and McLaren (1976) that competition for nest sites would increase in this community following its invasion by starlings 30 years ago by comparing nest site characteristics found in this study with similar data collected in 1959. Swallows now use significantly smaller cavities, bluebirds tend to use smaller but deeper cavities, and all species use cavities with a smaller entrance area. It is not clear, however, if these changes resulted from an intensification of competition or from a change in the resource available.

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RAPTOR ORGANIZATION REGISTRY

Statement of Purpose: Raptor is here defined as including all species of the traditional avian orders Falconiformes and Strigiformes. To borrow a statement from the British Trust for Ornithology (BTO News; December 1978) concerning the purpose of this registry, it "is an exercise in communication." There are, in the world, numerous splendid organizations whose major purpose is to deal with some aspect of the life of raptors, unfortunately their number, location(s), and specific purpose(s) are unknown to organizations and individuals with the need to know. The Raptor Research Foundation is interested in identifying locations and purposes of as many of these organizations as possible. Your cooperation in accomplishing this task would be greatly appreciated. It is RRF's intent to (1) assemble a document compiling the results, (2) provide each responding organization with a copy of this compilation to facilitate communication, and (3) make it available to other organizations (e.g., wildlife, conservation, and funding agencies).

Officers of organizations dealing with some aspect of the life of raptors are asked to submit the following information for inclusion in "A Directory of Raptor Organizations of the World": official organization name, address (permanent address if there is one), brief statement of purpose, approximate number of members, major area(s) of interest (e.g., basic research, captive breeding of raptors, conservation, education, falconry, general aspects, raptor movement, rehabilitation), name and official position of responding individual. This information should be forwarded (on organizational letterhead if one is available) to

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